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Abstract: Aims Functional traits are supposed to play an important role in determining the colonization success of new species into established communities. Short-term experimental studies have documented higher resistance of more diverse grasslands against colonization by new species. However, little is known about which traits colonizers should have to successfully invade diverse plant communities in the longer term and how community history may modify the resistance of diverse communities against colonization. **Methods** In a grassland biodiversity experiment (Jena Experiment) established with different species richness (SR; 1, 2, 4, 8 and 16) and functional group (FG) number and composition (1 to 4; legumes, grasses, small herbs, tall herbs), we studied colonization of naturally dispersed species in split-plots (i) with different duration of weeding (never weeded, weeded for 3 or 6 years and then un-weeded for 1 year) and (ii) with different duration of colonization (7 years, 4 years and 1 year after cessation of weeding). **Important Findings** Resistance against colonization by new species declined with increased duration of weeding (on average 13, 17 and 22 colonizer species in 1-, 4- and 7-year-old communities, respectively). Communities established at low diversity accumulated more colonizer species with a longer duration of weeding than more diverse communities. Duration of colonization had only small effects on the number of colonizer species. Colonizers with early successional traits, i.e. annual life cycle, reproduction by seeds, small seeds, long-lived seeds and an earlier start of a longer flowering period, were favoured in species-poor newly established experimental plant communities (short duration of weeding) and early after cessation of weeding (short duration of colonization). A change from early- to mid-successional traits, i.e. taller growth, perennial life cycle, vegetative reproduction, characterized colonization at increased plant diversity and in communities with legumes or without grasses. Legume absence/grass presence and increased duration of weeding led to a shift in colonizer strategies from rapid nutrient uptake and cycling (higher specific leaf area) to nutrient retention and symbiotic N₂ fixation. Our study shows that non-random trait spectra of naturally dispersed colonizers encompass trade-offs between different functions (reproduction, persistence, growth) reflected in a change from early- to mid-successional traits at increasing plant diversity, with a longer duration of weeding and a longer time of colonization.

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Plant diversity and community history shift colonization success from early- to mid-successional species

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Abstract

Aims

Functional traits are supposed to play an important role in determining the colonization success of new species into established communities. Short-term experimental studies have documented higher resistance of more diverse grasslands against colonization by new species. However, little is known about which traits colonizers should have to successfully invade diverse plant communities in the longer term and how community history may modify the resistance of diverse communities against colonization.

Methods

In a grassland biodiversity experiment (Jena Experiment) established with different species richness (SR; 1, 2, 4, 8 and 16) and functional group (FG) number and composition (1 to 4; legumes, grasses, small herbs, tall herbs), we studied colonization of naturally dispersed species in split-plots (i) with different duration of weeding (never weeded, weeded for 3 or 6 years and then un-weeded for 1 year) and (ii) with different duration of colonization (7 years, 4 years and 1 year after cessation of weeding).

Important Findings

Resistance against colonization by new species declined with increased duration of weeding (on average 13, 17 and 22 colonizer species in 1-, 4- and 7-year-old communities, respectively). Communities established at low diversity accumulated more colonizer species with a longer duration of weeding than

more diverse communities. Duration of colonization had only small effects on the number of colonizer species. Colonizers with early successional traits, i.e. annual life cycle, reproduction by seeds, small seeds, long-lived seeds and an earlier start of a longer flowering period, were favoured in species-poor newly established experimental plant communities (short duration of weeding) and early after cessation of weeding (short duration of colonization). A change from early- to mid-successional traits, i.e. taller growth, perennial life cycle, vegetative reproduction, characterized colonization at increased plant diversity and in communities with legumes or without grasses. Legume absence/grass presence and increased duration of weeding led to a shift in colonizer strategies from rapid nutrient uptake and cycling (higher specific leaf area) to nutrient retention and symbiotic N₂ fixation. Our study shows that non-random trait spectra of naturally dispersed colonizers encompass trade-offs between different functions (reproduction, persistence, growth) reflected in a change from early- to mid-successional traits at increasing plant diversity, with a longer duration of weeding and a longer time of colonization.

Keywords: abundance-weighted community mean traits, biodiversity, colonization, simple community mean traits, species richness

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INTRODUCTION

The processes which determine the number and composition of co-occurring species have been controversially discussed for a long time in ecology (Diamond 1975; Weiher and Keddy 1995). Mechanisms affecting the colonization of species as well as mechanisms permitting species to persist after colonization are particularly relevant for a better understanding of community assembly. In addition to the local environment, biotic interactions and niche differentiation, the pool of available species in the surroundings and their ability to disperse influence colonization. According to this deterministic view, plant functional characteristics are assumed to play an important role in community assembly (Díaz *et al.* 1998; Westoby and Wright 2006), but there is an ongoing debate on the importance of deterministic versus neutral processes (Hubbell 2001). The neutral theory is based on the assumption that stochasticity in colonization and extinction processes creates community assembly patterns. Niche-based and neutral processes are not mutually exclusive (Gravel *et al.* 2006).

The basic tasks plants have to fulfil after colonization are persistence, growth and reproduction (Weiher *et al.* 1999). Different functional traits are associated with these basic tasks and related to different niche axes (Violle *et al.* 2007). Following the niche-based concept, plant functional traits not only should explain the success or failure (i.e. presence–absence probability) of a species, but also may control the abundance of species present in a community (Cornwell and Ackerly 2010). If species possessing favourable attributes are more abundant, a different weighting of species when deriving community means from traits should reflect this process. If more importance is given to the minor species by assigning them the same weight as the more abundant species (simple averaging; e.g. Fonseca *et al.* 2000), presence–absence probabilities are reflected more adequately. Weighting species according to their relative abundances (weighted averaging; Garnier *et al.* 2004) emphasizes the traits of the more abundant species (Cingolani *et al.* 2007).

Resistance against the colonization by new species is not an inherent community characteristic, but may fluctuate dependent on environmental conditions, interactions among resident species themselves and the available pool of potential colonizers (Davis *et al.* 2005). Empirical evidence from short-term experimental studies suggests higher resistance of more diverse plant communities against the spontaneous colonization by new species (e.g. Knops *et al.* 1999; Lanta and Lepš 2008; Roscher *et al.* 2009), but the role of community history in shaping the relationship between plant diversity and the number and functional characteristics of colonizer species have not been considered so far. In general, it may be assumed that traits related to colonization ability (i.e. early successional traits such as annual life cycle, early flowering, reproduction by seeds, small seeds) determine presence–absence probabilities and abundances of species in newly established vegetation with more suitable niches for colonization, while competition- and persistence-related traits (typical for mid-successional stages of herbaceous vegetation such as

taller growth, vegetative reproduction) are more important for colonizer success in established vegetation at later stages (Garnier *et al.* 2004; Pywell *et al.* 2003; Thompson *et al.* 2001). Higher colonization resistance of more diverse communities has been explained by a more complete resource use leaving fewer resources for colonizers (Fargione and Tilman 2005). Therefore, it is likely that competition-related traits also become more important as characteristics of successful colonizers at increased plant diversity.

In the present study, we used a grassland biodiversity experiment (Jena Experiment; Roscher *et al.* 2004) to establish split-plots, where weeding was stopped at different times after sowing. We studied effects of plant diversity on the colonization of naturally dispersed species in (i) communities opened for colonization at different age (i.e. never weeded, weeded for 3 or 6 years and then un-weeded for 1 year = different duration of weeding) and (ii) in communities of the same age opened a different length of time for colonization (=different duration of colonization) to test the hypotheses that (i) the colonization of a higher number of species and species with early successional traits is favoured after a shorter duration of weeding (newly established plant communities) and after a shorter duration of colonization, (ii) the colonization of fewer species and species with mid-successional traits is more likely after a longer time of weeding or a longer duration of colonization and (iii) that higher sown plant diversity changes the colonization success from early- to mid-successional species.

MATERIALS AND METHODS

Design of the Jena Experiment

The site of the Jena Experiment (Roscher *et al.* 2004) is located on the floodplain of the Saale river at the northern edge of Jena (Thuringia, Germany; 50°55'N, 11°35'E, 130 m a.s.l.) and was used as a highly fertilized arable field for the last 40 years prior to the establishment of the biodiversity experiment in 2002. The area around Jena is characterized by a mean annual air temperature of 9.3°C and an annual precipitation of 587 mm (Kluge and Müller-Westermeier 2000). The soil is a nutrient-rich riverside soil (Eutric fluvisol) developed from up to 2-m-thick loamy fluvial sediments. Due to the fluvial dynamics of the Saale river, the field covers a gradient in soil characteristics; soil texture ranges from sandy loam near the river to silty clay with increasing distance from the river.

The studied system represents Central European mesophilic grasslands traditionally used as hay meadows (Arrhenatherion community; Ellenberg 1988). The 60 experimental species were classified into four FGs based on a cluster analysis of a literature-based matrix of morphological and ecological traits: 16 grasses, 12 legumes, 12 small herbs and 20 tall herbs (Roscher *et al.* 2004). The experimental design crossed the factors plant SR (1, 2, 4, 8 and 16) and number of plant FGs (1, 2, 3 and 4 FGs) as orthogonally as possible. There are 16 replicates for monocultures (1 FG), 16 for two-species mixtures (1 or 2 FGs), 16 for four-species mixtures (1–4 FGs), 16 for eight-species mixtures (1–4 FGs) and 14 for sixteen-species

mixtures (1–4 FGs, with the limitation that there were not enough legume or small-herb species to create mono-functional 16-species mixtures of these 2 FGs), resulting in a total of 78 plots of 20 × 20 m size. The plots were assembled in four blocks in parallel to the river to account for the gradient in soil characteristics.

Three subplots of 2.00 × 2.25 m size were established at 0.5 m distance from the plot margin in each large plot of the biodiversity experiment (Roscher et al. 2009). One of these subplots was never weeded since the establishment of the experiment in 2002, while unwanted species not belonging to the sown species combinations were weeded twice per year (April and July) in two subplots. Three years after sowing, in 2005, one previously weeded subplot was selected at random in each plot where weeding was stopped. Six years after sowing, in 2008, weeding was discontinued in the third subplot resulting in the following treatments:

- CO: never weeded since sowing in 2002 ('old stage colonization')
- CM: weeding discontinued after 3 years in 2005 ('middle stage colonization')
- CY: weeding discontinued after 6 years in 2008 ('young stage colonization').

All plots were mown twice a year (June and September) to 5 cm height corresponding to the management of extensive hay meadows in the study area. Plots were not fertilized throughout the experiment. The plot area surrounding the split-plots used for the present study was regularly weeded in two campaigns per year (April and July) to remove species not sown into a particular plot.

Data collection

Colonizer SR and identities were recorded four times per year, at the start of the growing season (early April), shortly before first mowing (late May), shortly after first mowing (July) and shortly before second mowing (late August). Per-species cover was estimated during the inventories in late May and August using a modified decimal scale (Londo 1976). Numerical values for species cover were coded as 0.5 (<1%), 3 (1–5%)

10 (6–15%), 20 (16–25%), 30 (26–35%), 40 (36–45%), 50 (46–55%), 60 (56–65%), 70 (66–75%), 80 (76–85%) and 90 (>85%).

A trait matrix was compiled from the literature (Rothmaler 2002) and several databases (LEDA: Kleyer et al. 2008; BiolFlor: Klotz et al. 2003) for all colonizer species (180 species in total). Plant traits were selected to cover various aspects of plant functioning relevant for persistence, growth and reproduction (Table 1). To complement data on specific leaf area (SLA) for missing species, bulk samples of 10–20 fully expanded sun leaves per species were collected at the field site or in surrounding habitats in 2009. Leaf area was measured with a leaf area meter (LI-3100 Area Meter; LI-COR, Lincoln, USA) and samples were weighed after drying (48 h, 70°C) to derive SLA as the ratio of total leaf area divided by total leaf mass per sample ($\text{mm}^2_{\text{leaf}}/\text{mg}_{\text{leaf}}$).

Data analyses

All data were analyzed in two subsets. First, effects of duration of weeding were evaluated by analyzing subplots that had been opened for colonization in 2002 (CO), 2005 (CM) or 2008 (CY) 1 year later, i.e. in 2003, 2006 or 2009, respectively, for colonization of new species. We use the synonym 'community age' for duration of weeding with the following equivalencies: CO2003 = never weeded = 1-year old community, CM2006 = 3 years of weeding = 4-year old community, CY2009 = 6 years of weeding = 7-year old community. Second, effects of duration of colonization were evaluated by analyzing the same subplots CO, CM or CY in 2009, i.e. 7 years, 4 years or 1 year after cessation of weeding, respectively, for colonization of new species (accumulated over 7 years, 4 years or 1 year of colonization: CO2009, CM2009, CY2009). Note that the same data were used for CY2009 in both analyses.

To quantify community-level functional characteristics of colonizers, first abundance-weighted community mean traits (CWM) were calculated using the observed maximum cover abundance of each colonizer species *i* per year and subplot as

Table 1: overview of plant traits used in analyses of community mean traits compiled from different sources and trait data availability

Variable	Type of variable	Source	Availability (%)
Seed longevity	Continuous (between 0 and 1)	LEDA (Kleyer et al. 2008)	94
Seed mass	Continuous	BiolFlor (Klotz et al. 2003)	94
Start of flowering	Ordinal: 1 = before May; 2 = May; 3 = June; 4 = July	Rothmaler (2002)	99
Duration of flowering	Ordinal: 1 = 2 months or less; 2 = 3 months; 3 = 4 months; 4 = more than 4 months	Rothmaler (2002)	99
Reproduction by seed	Binary: 0 = vegetative and by seed; 1 = exclusively by seed	BiolFlor (Klotz et al. 2003)	100
Life cycle annual	Binary: 0 = biennial, monocarpic perennial or perennial; 1 = annual	Rothmaler (2002)	100
Plant height	Continuous (m)	BiolFlor (Klotz et al. 2003)	100
SLA	Continuous ($\text{mm}^2_{\text{leaf}}/\text{mg}_{\text{leaf}}$)	LEDA (Kleyer et al. 2008), own measurements	95
N ₂ fixation	binary: 0 = none; 1 = yes	Rothmaler (2002)	100

$$CWM = \sum_{i=1}^S p_i t_i \quad (1)$$

where t_i is the trait value of species i , p_i is the proportional abundance of species i and S is the number of species in a subplot (Garnier *et al.* 2004). Second, simple community mean traits (CM) were computed by equal weighting of all colonizer species as

$$CM = \frac{1}{S} \sum_{i=1}^S t_i \quad (2)$$

Colonizer species numbers and abundance-weighted community mean traits (CWM) were analysed with generalized linear models (sequential sum of squares). The design of the Jena Experiment is near-orthogonal based on gradients in SR and FG number, but it is not possible to achieve a fully balanced design because FG number cannot exceed species number. Therefore, the fitting sequence of variables followed the a priori hypotheses of the biodiversity experiment. In analyses across the diversity gradient, the block was followed by a log-linear term for sown SR, a linear term for FG number (FG), a split-plot term either for duration of weeding (comparing communities of different age opened the same time for colonization) or for duration of colonization (comparing

communities of the same age opened a different length of time for colonization) and its interaction with SR and FG. In series of analyses, contrasts for the presence/absence of each FG were fitted after the terms for SR and FG to assess the proportion of residual variation attributable to effects of particular FGs. Analyses were extended by introducing an additional level *weighting* nested in split-plots for comparison of abundance-weighted (CWM) and simple (CM) community mean traits. Data analyses were performed with the statistical software R (Version 2.11.1, R Development Core Team, <http://www.R-project.org>).

RESULTS

Effects of sown plant diversity and of duration of weeding and duration of colonization on the number of colonizer species

The number of colonizer species was always higher in communities initially sown with a lower rather than higher number of species or FGs (Fig. 1a and d). The lower resistance of species-poor communities to colonization by new species was more pronounced when communities had been weeded for a longer time, potentially due to a deterioration of species-poor communities over time (Table 2).

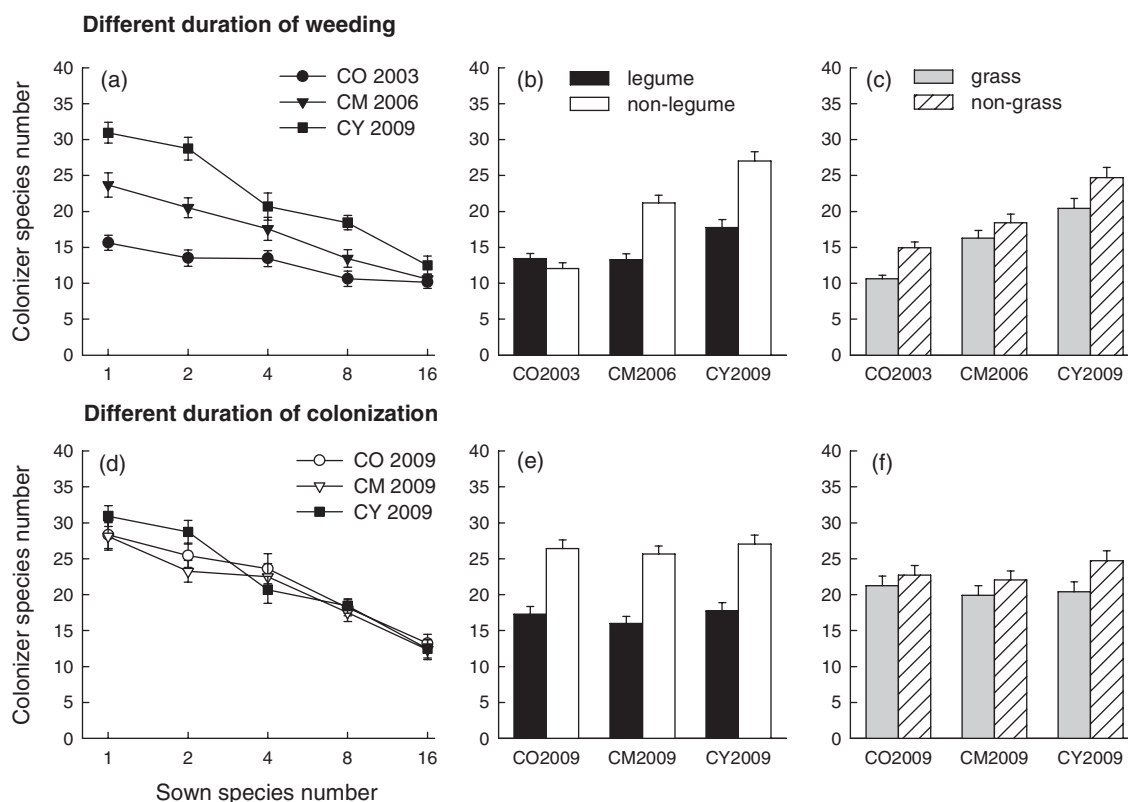


Figure 1: numbers of colonizer species after cessation of weeding as a function of sown plant SR (a, d), dependent on the presence of legumes (b, e) and dependent on the presence of grasses (c, f) in the sown plant communities. Values are arithmetic means (± 1 SE) per sown SR level (a, d), with/without legume species (b, e) and with/without grass species (c, f) after different duration of weeding (a–c) and after different duration of colonization (d–f).

Table 2: ANOVA of colonizer species numbers in communities after different duration of weeding and after different duration of colonization

Duration of weeding					Duration of colonization				
Colonizer species number					Colonizer species number				
Source of variation	df	MS	F	P	Source of variation	df	MS	F	P
Block	3	136.6	3.84	0.013	Block	3	146.0	1.62	0.192
SR (log-linear)	1	4527.4	127.16	<0.001	SR (log-linear)	1	7504.5	83.28	<0.001
FG (linear)	1	182.3	5.12	0.027	FG (linear)	1	418.1	4.64	0.035
LE	1	394.5	12.91	<0.001	LE	1	2285.3	38.60	<0.001
GR	1	3.0	0.08	0.774	GR	1	449.4	5.28	0.024
SH	1	97.3	2.80	0.099	SH	1	291.5	3.34	0.072
TH	1	75.4	2.15	0.147	TH	1	115.1	1.28	0.261
Plot	72	35.6			Plot	72	90.1		
DurWeed	2	1868.3	101.26	<0.001	DurCol	2	48.4	5.22	0.006
DurWeed × SR	2	422.2	22.88	<0.001	DurCol × SR	2	50.6	5.46	0.005
DurWeed × FG	2	89.4	4.85	0.009	DurCol × FG	2	31.6	3.40	0.036
DurWeed × LE	2	387.4	28.77	<0.001	DurCol × LE	2	27.9	3.09	0.048
DurWeed × GR	2	217.4	13.79	<0.001	DurCol × GR	2	5.4	3.39	0.564
DurWeed × SH	2	28.8	1.57	0.211	DurCol × SH	2	0.5	0.07	0.992
DurWeed × TH	2	6.6	0.35	0.702	DurCol × TH	2	9.2	0.99	0.375
Residuals	150	18.5			Residuals	150	9.3		

Model terms were fitted sequentially and tested against the respective residuals. Note that FG identities and their interactions with duration of weeding and duration of colonization, respectively, were fitted as separate contrasts in series of analyses. Given are the degrees of freedom (df), mean sums of squares (MS), *F* ratios (*F*) and *P* values (*P*). Arrows indicate increases (↑) or decreases (↓) of colonizer species numbers in response to the predictor variables. Abbreviations: ANOVA = analysis of variance, DurCol = duration of colonization (CO2009, CM2009, CY2009), DurWeed = duration of weeding (CO2003, CM2006, CY2009), FG = sown functional group number, GR, grass, LE, legume, SH, small herb, SR = sown species number, TH, tall herb.

Duration of weeding, i.e. years for which a community was weeded prior to opening it for colonization, had significant effects on the number of colonizer species. The number of colonizer species was lower in younger than in older experimental communities weeded for several years (mean \pm 1 SE: CO2003 = 12.7 ± 0.5 ; CM2006: 17.3 ± 0.8 ; CY2009: 22.5 ± 1.0 ; Fig. 1a, Table 2). Duration of colonization, i.e. years for which a community was allowed to be colonized prior to assessment, had significant but smaller effects on the number of colonizer species. Interestingly, the number of colonizer species did not increase with longer duration of colonization and in fact, it was highest in the communities most recently opened for colonization (CO2009 = 22.0 ± 0.9 ; CM2009: 21.0 ± 0.9 ; CY2009: 22.5 ± 1.0 ; Fig. 1d, Table 2).

Duration of weeding modulated the effects of legumes: after a short duration of weeding (1 year), legume presence increased colonization of new species, but effects of legumes reversed and less colonizer species settled in communities with legumes when weeding was stopped after several years (Table 2, Fig. 1b). Positive effects of grasses on the suppression of colonizers also depended on duration of weeding: after a shorter duration of weeding, differences between communities sown with grasses and communities sown without grasses were stronger than after several years of weeding (Table 2, Fig. 1c).

Effects of sown plant diversity on mean trait values of colonizer species

Abundances of small-seeded colonizers with long-lived seeds increased in communities with a higher number of sown species and FGs and in communities containing legumes, while abundances of colonizers with the opposite characteristics (larger seeds, short-lived seeds) increased in communities containing grasses (online supplementary Table S1, Figs 2a and b and 3a and b). Abundances of colonizers with a later start of a shorter flowering period increased (Fig. 2c and d), and abundances of colonizers with an annual life cycle and reproduction by seeds declined (Fig. 2e and f) at higher numbers of sown species and FGs. Abundances of colonizers with an annual life cycle also decreased in communities with legumes (Fig. 3f). Increased species and FG richness or legume presence favoured colonizers with a taller growth (Figs 2g and 3g). Colonizers in communities with legumes had higher SLA (Fig. 3h). Legume presence reduced the colonization of further N_2 fixing legume species, while grass presence had the opposite effects (Fig. 3i). While duration of weeding and duration of colonization only marginally affected variation in colonizer trait characteristics in response to increased species or FG richness, the effects of sown legumes or grasses often changed in strengths and direction dependent on duration

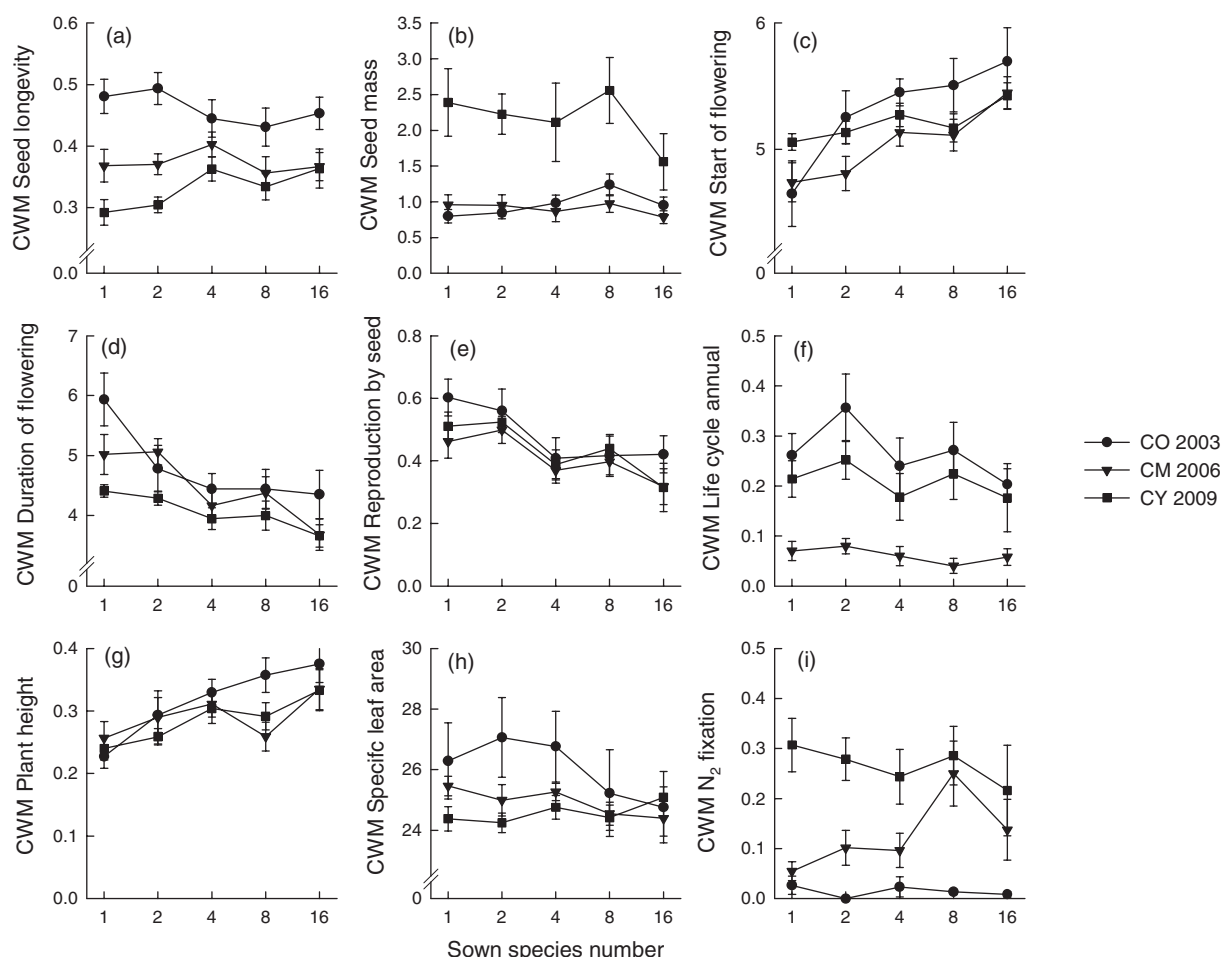


Figure 2: abundance-weighted community means for (a) seed longevity, (b) seed mass, (c) start of flowering, (d) duration of flowering, (e) mode of reproduction (mainly via seeds), (f) annual life cycle, (g) plant height, (h) SLA and (i) species ability for N₂ fixation. Values are arithmetic means (± 1 SE) per sown SR level for colonizer assemblages after different duration of weeding.

of weeding before allowing colonization of new species (significant interaction LE \times D, GR \times D in [online supplementary Table S1A, Fig. 3](#)).

Effects of duration of weeding and duration of colonization on mean trait values of colonizer species

From a total of 170 species colonizing communities in the first year after cessation of weeding, 37% occurred at all stages, while 28% were only present at a single stage of community age (i.e. weeding duration 0, 3 years or 6 years). In contrast, from a total of 146 species that had colonized the communities and were still present in 2009, 60% occurred at all stages, while 23% only occurred at a single stage of colonization (duration of colonization 7 years, 4 years or 1 year). A long duration of weeding decreased the abundance of colonizers with long-lived seeds, later start and longer duration of flowering, annual life cycle, reproduction by seeds and higher SLA

([online supplementary Table S1A, Fig. 2](#)). A long duration of weeding led to a shift in favour of colonizers with a perennial life cycle and the ability for vegetative spread; in addition, N₂ fixing legumes obtained higher abundances as colonizers. Duration of colonization had smaller effects on mean trait values of colonizer species than did duration of weeding ([online supplementary Table S1B](#)): species with long-lived seeds, reproduction by seeds, an earlier start and longer duration of flowering were favoured in communities that were most recently (2008) opened for colonization.

Comparison between effects of sown plant diversity, duration of weeding and duration of colonization

Although plant diversity and duration of weeding or duration of colonization had significant effects on colonizer trait characteristics, the fraction of explained variation differed considerably. Plant diversity explained 10–18% of variation in mean

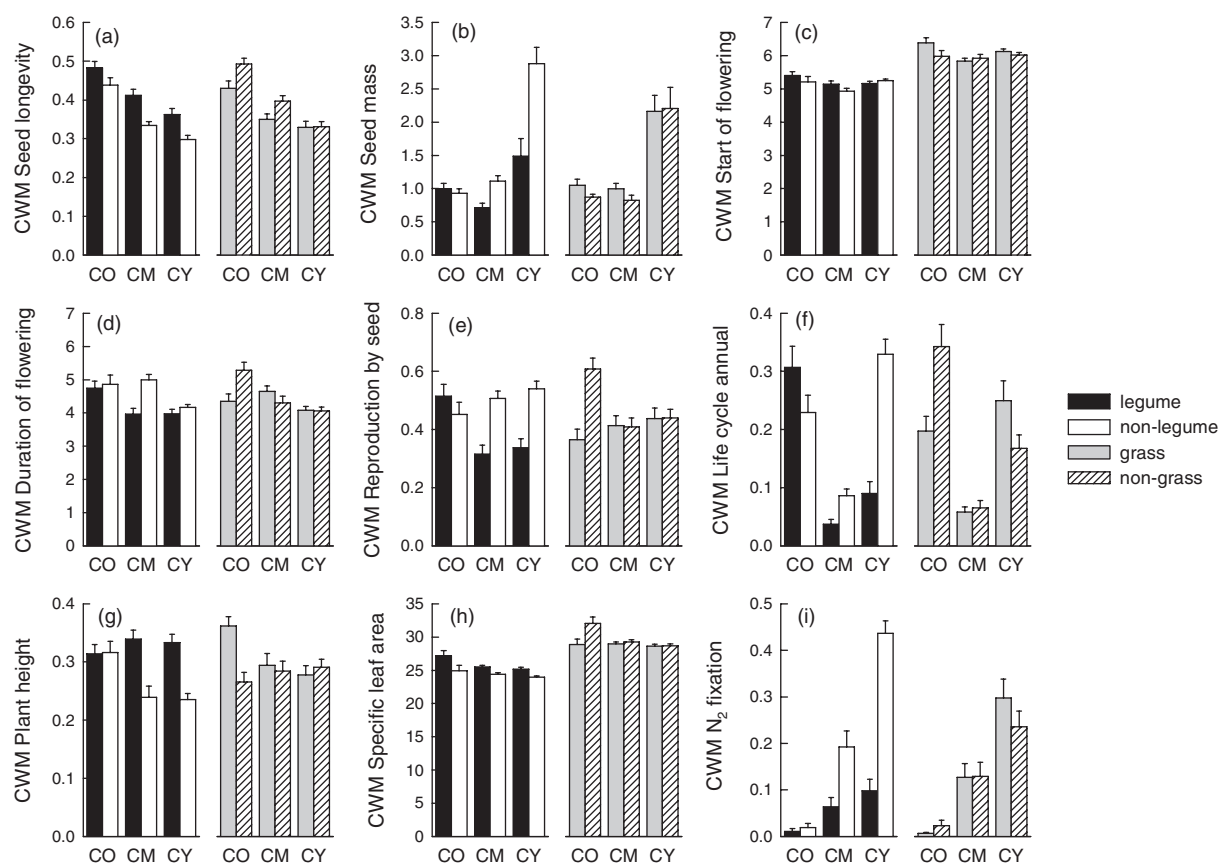


Figure 3: abundance-weighted community means for (a) seed longevity, (b) seed mass, (c) start of flowering, (d) duration of flowering, (e) mode of reproduction (mainly via seeds), (f) annual life cycle, (g) plant height, (h) SLA and (i) species ability for N_2 fixation. Values are arithmetic means (± 1 SE) for communities with/without legume species and with/without grass species respectively for colonizer assemblages after different duration of weeding.

traits of colonizer assemblages in communities with different duration of weeding before allowing the colonization of new species, while plant diversity accounted for 26–45% of variation in mean traits of colonizer assemblages in communities with different duration of colonization (Fig. 4). Duration of weeding explained 25–30% of variation in colonizer characteristics such as seed longevity, seed mass, life cycle and the ability for N_2 fixation and <5% of variation in other traits. The fraction of variation attributable to differences in plant diversity–colonizer trait relationships after different duration of weeding was dependent on trait identity and amounted to 3–18% (Fig. 4a). In contrast, the fraction of variation in colonizer trait characteristics explained by duration of colonization was near negligible (Fig. 4b).

Abundance-weighted versus simple community means of colonizer traits

Differences in abundance-weighted (CWM) and simple (CM) community means of most traits showed that abundant colonizers differed in trait composition from the average across all

species (Fig. 5, online supplementary Table S2). Abundance-weighted means for seed longevity and SLA were larger and abundance-weighted means for seed mass were smaller than simple means, indicating that species with longer-lived seeds, smaller seeds and higher SLA reached higher dominance than species with the opposite characteristics (Fig. 5a, b and h). Furthermore, abundance-weighted means for start of flowering, reproduction by seeds and a short life cycle were lower than simple means (Fig. 5c, e and f) when colonization of new species started after a short duration of weeding, suggesting that the presence probabilities of species with these characteristics were greater than their chance to obtain dominance. In contrast, abundance-weighted means for a short life cycle, a late start of a short flowering period, tall growth and the ability for N_2 fixation (Fig. 5c, d, f, g and i) deviated positively from simple means in later years irrespective of duration of colonization. Sown plant diversity (SR, FG number, presence–absence of grasses, legumes) had additional effects on differences between abundance-weighted and simple means of colonizer traits (online supplementary Table S2).

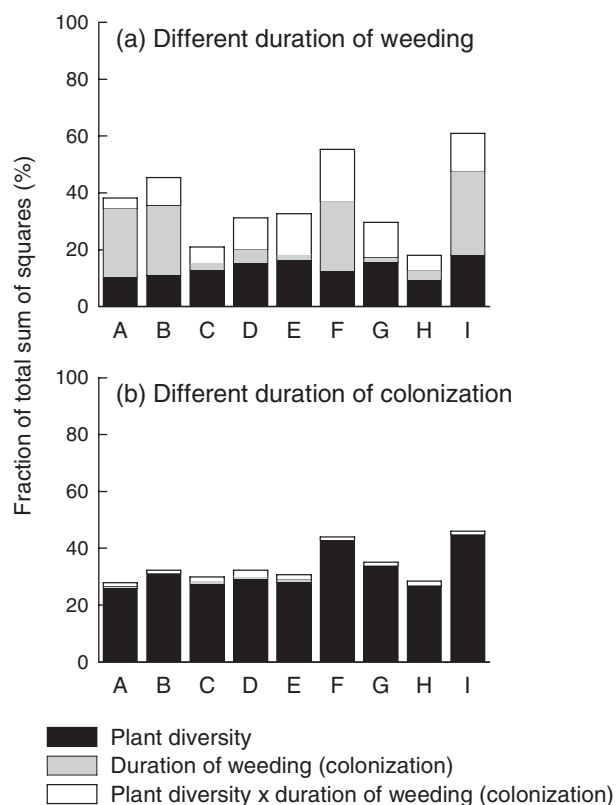


Figure 4: proportion of variation explained by plant diversity (SR, FG richness and presence-absence of particular FGs), community history, i.e. (a) duration of weeding and (b) duration of colonization, and the interaction between plant diversity and community history. (A) Seed longevity (B) Seed mass (C) Start of flowering (D) Duration of flowering (E) Reproduction by seed (F) Life cycle (G) Plant height (H) Specific leaf area (I) N₂ fixation.

DISCUSSION

Efforts to identify characteristics of species that warrant an intrinsic colonization advantage led to the conclusion that there exists no universal suite of traits reliably predicting colonization success (Davis *et al.* 2005). With respect to the questions addressed in the present study, we found that the suites of traits that afford successful colonization of naturally dispersed species are not ubiquitous, but depend on a match between characteristics of colonizer species and the diversity and history of the invaded community.

Number of colonizer species

Invasion studies in regularly weeded experimental communities have been criticized because sustained disturbance through weeding could result in communities which are more susceptible to colonization of new species (Wardle 2001). This was confirmed to some extent in our study as explained below. First of all, however, our study corroborated earlier observations (Hector *et al.* 2001; Knops *et al.* 1999; Roscher *et al.* 2009) that plant communities initially sown with a larger species number were spontaneously colonized by a lower number of species (Fig. 1a and d). In addition,

both duration of weeding previous to the start of colonization as well as duration of colonization (corresponding to different time since cessation of weeding) modified the strength of plant diversity effects on colonization of new species. Particularly, plant communities sown with a lower number of species and weeded for a longer time before allowing colonization by new species were colonized by a larger number of species, which even exceeded the number of colonizer species in subplots open a longer time for colonization by new species (see CY2009 in Fig. 1a and d). Nevertheless, the lower stability of monocultures and low-diversity communities even in the absence of weeding or with short duration of weeding (see also Roscher *et al.* 2013) indicates that it was not mainly the weeding disturbance that led to increased colonization of these communities. Although the cover of sown species explained variation in the number of colonizer species in the present study (analysis not shown), the effects of sown plant diversity and community history on the number of colonizer species were not simply attributable to changes in residents' community characteristics. The observed increasing strength of plant diversity effects on colonization resistance over time was probably due to imbalanced depletion of resources and the accumulation of soil-borne pathogens (Klironomos 2002; Marquard *et al.* 2013; Schenk 2006). In addition, changes in the available species pool may abet the increasing accumulation of colonizer species in low-diversity communities. In the early phase of the Jena Experiment, which was established on a former agricultural field, colonizers mainly emerged from the soil seed bank before dispersal from neighbouring plots and the surroundings increased the potential number of colonizer species in low-diversity communities disproportionately (Roscher *et al.* 2009). Eventually, competition between colonizers even limited the coexistence of a higher number of colonizer species and might explain lower numbers of colonizer species with an increasing duration of colonization (Fig. 1d).

Surprisingly, a longer duration of weeding reversed effects of legumes on the number of colonizer species from positive to negative relationships. Allelopathy arising from phenolic compounds of legume residues (Dyck and Liebman 1994; Ohno and Doolan 2001) or harmful effects of legumes on microbial protection against soil-borne pathogens (Latz *et al.* 2012) could explain the lower probability of new species to colonize communities with legumes over several years.

Mean trait values of colonizer species

Communities that had been weeded only for a short length of time were colonized in the first year after cessation of weeding by species with an annual life cycle. Early successional species usually do not spread vegetatively but produce a larger amount of persistent seeds (Huston and Smith 1987; Kahmen and Poschlod 2004; Prach *et al.* 1997). Seed mass increases during secondary succession (Huston and Smith 1987; Navas *et al.* 2010) and small-seeded species are particularly successful in early stages of colonization (Milbau *et al.* 2003; Thompson *et al.* 2001). Indeed, abundance-weighted

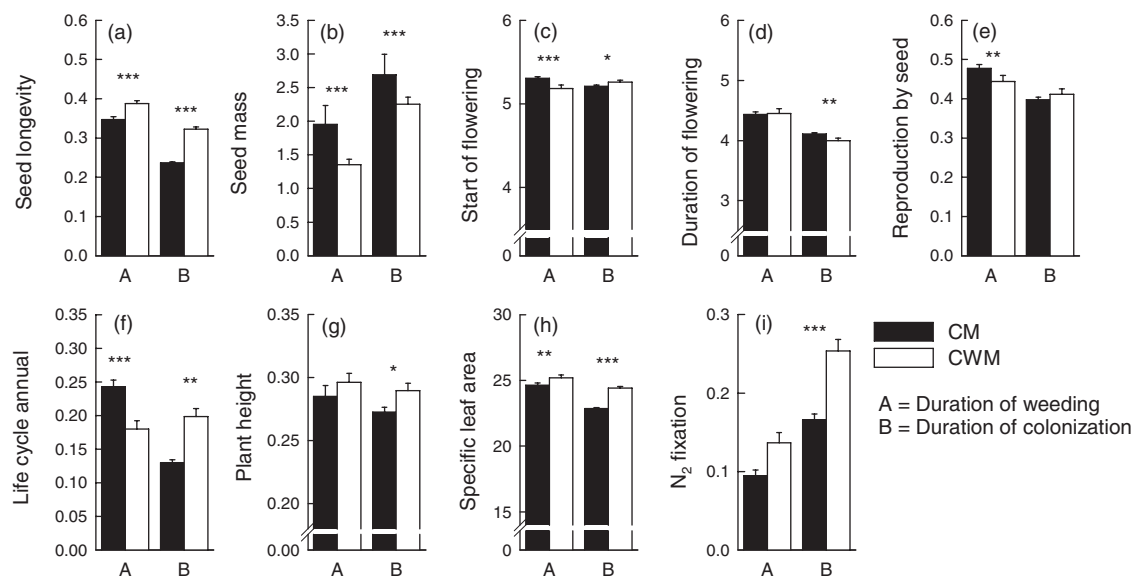


Figure 5: simple (CM) and abundance-weighted (CWM) community means of (a) seed longevity, (b) seed mass, (c) start of flowering, (d) duration of flowering, (e) mode of reproduction (mainly via seeds), (f) annual life cycle, (g) plant height, (h) SLA and (i) ability for N₂ fixation. Values are arithmetic means (± 1 SE) across communities after different duration of weeding (CO2003, CM2006, CY2009) and after different duration of colonization (CO2009, CM2009, CY2009), respectively. Results of analysis of variance ([online supplementary Table S2](#)) testing for differences between simple and abundance-weighted community mean traits (CM vs. CWM) are indicated with: * $P \leq 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

means of colonizer traits revealed that regeneration strategies of early successional species (small seeds, longer-lived seeds) characterized early phase of colonization and in particular colonization after a short duration of weeding. Colonizers with more conservative resource-use strategies (lower CWM in SLA; [Garnier et al. 2007](#)) or the ability to fix atmospheric N₂ were more successful in communities with a longer history of weeding.

Functional trait composition in response to increased plant diversity also reflected a colonization/competition trade-off ([Tilman 1994](#)) and a transition from early to later herbaceous stages of secondary succession ([Vile et al. 2006](#)). In a previous study, we showed that increased plant diversity supports the selection of clones with K-strategy traits in offspring of the most abundant colonizer species in our experiment, *Taraxacum officinale* Wiggers ([Lipowsky et al. 2012](#)). In the present study, we found more colonizers with a short life cycle (r-strategy traits) in plant communities sown with a lower species and FG number, while perennials with the ability for vegetative spread and taller growth (K-strategy traits) were more successful as colonizers in more diverse communities. At higher SR, competition for light and nutrients increases. Shifts in favour of taller species often indicate a response to increasing light competition (e.g. [Kahmen and Poschold 2004](#); [Vile et al. 2006](#)). Establishment of large-seeded species is less suppressed in grassland vegetation compared to small-seeded species ([Burke and Grime 1996](#); [Kotorová and Lepš 1999](#)). Nevertheless, small-seeded species with longer-lived seeds reached higher abundances as colonizers in plant communities of increased SR. Because of a trade-off between dispersal

success (related to large seed numbers) and establishment success (related to large seed size; [Turnbull et al. 1999](#)) seed size is not necessarily a good predictor for colonization success in the longer term. In our study, we did not differentiate between seedling establishment of colonizers and adult success, but compared the colonizer composition of communities being at least the second year open for colonization. [Thompson et al. \(2001\)](#) found that regenerative traits (seed mass, germination characteristics) are good predictors for colonization of grasslands along a fertility-disturbance matrix in the first 2 years, while after 5 years, no single trait was related to colonization success.

Furthermore, legume presence generally strengthened effects of sown plant diversity by favouring colonizers with trait combinations consistent with those in more diverse communities. Higher community-level means in growth height and SLA indicated that colonizers with traits associated with higher competitiveness in more fertile environments were more successful in communities with legumes. In addition, colonizers with smaller seeds and longer-lived seeds were more abundant in communities with legumes. Opposite effects were observed in communities with grasses. These results are in accordance with a previous short-term seed addition study in the Jena Experiment ([Roscher et al. 2009](#)). Thus, it is likely that legumes and grasses had detrimental effects on the establishment of colonizers with particular propagule characteristics. For example, in communities with legumes, germination might have been inhibited by allelopathic compounds, high soil CO₂ concentration due to high root respiration ([Hilhorst and Karssen 2000](#)) and

accumulated soil-borne pathogens; additionally, increased soil heterotrophic activity might have reduced the number of germinable colonizer seeds through burial and feeding (Eisenhauer *et al.* 2008).

Our analyses of communities with different history revealed that duration of weeding had noticeable effects on the relationships between plant diversity and mean trait values of colonizers (Fig. 4a), while duration of colonization only explained a small proportion of variation in colonizer traits (Fig. 4b). Differences in simple and abundance-weighted community mean traits (Fig. 5) indicated that presence-absence probabilities of colonizer species were mainly determined by traits related to regeneration (e.g. life cycle, seed mass, reproduction by seeds), while colonizer abundances were related to traits characterizing persistence (seed longevity) and growth (plant height, SLA, N₂ fixation).

Our study shows that trait spectra of naturally dispersed colonizers in response to plant diversity and community history are not random, but encompass trade-offs between different functions (reproduction, persistence, growth) which are typically found in early- and mid-successional stages of herbaceous vegetation.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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